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Ecomorphology of Bats: Comparative and Experimental Approaches Relating Structural Design to Ecology

Sharon M. Swartz, Patricia W. Freeman, and Elizabeth F. Stockwell

Introduction

Interconnections between morphological design and function are central to biology; they underlie natural patterns in species distribution, phylogenetic diversification, and morphological specialization. At its core, ecomorphology explores the causal relationships between organismal design and behavioral performance and investigates how these relationships influence an organism's ability to exploit its environment. To the extent that we can understand mechanisms that dictate these relationships, we can gain broad insight into the ecology and evolution of species, higher-order clades, and ecological assemblages.

The past several decades have seen the beginning of integration of discoveries in the ecology and morphology of bats into an ecomorphological whole that promises to be greater than the sum of its parts. However, achieving this integration is challenging. Each of the elements of this interdisciplinary field is, in itself, a vast and complex subject. This book is a testament to the breadth and depth of ecological studies of bats. Morphological studies now extend beyond descriptive anatomy in both outlook and method, and incorporate, for example, aspects of genetics, physiology, solid and fluid mechanics, and developmental biology. There is also greater awareness that a particular morphology embodies not only the requirements of present life but also an organism's developmental and evolutionary history.

In ecomorphological analysis, one seeks to establish the nature and strength of the relationship between morphology and ecology. The relationship between an animal's structure and its interactions with its environment may itself be complicated and multifactorial. Morphology dictates an individual's performance limits and restricts its behavioral repertoires; regardless of habitat, a bat cannot fly faster or eat larger prey than its anatomy will allow. However, while morphology may constrain potential activities, the ecology of an animal is also strongly influenced by the local environment in which it

functions day to day; flight speeds employed may be dictated primarily by the nature of the three-dimensional spatial environment, while prey selection may be driven by availability and abundance.

Part of the intrinsic challenge of the study of ecomorphology is that it is fundamentally synthetic. This complex subject draws on diverse conceptual approaches, integrates data from the field, the laboratory, and the museum, and takes into account both ecological and evolutionary timescales. Moreover, the volant, nocturnal lifestyles of bats present exceptional methodological challenges. Nonetheless, steadily increasing basic knowledge of bat biology along with a growing repertoire of conceptual and methodological approaches have set the stage for unprecedented innovations in the next few years.

Here, we examine recent advances in the study of the relationships among morphology, behavior, and ecology of bats. In this chapter, we provide one view of ecomorphology as a discipline, and highlight some case studies of particular relevance to understanding how the morphology of bats relates to their ecology, with special attention to the structure of the feeding apparatus, particularly the teeth and skull, in relation to dietary preferences, and the morphology of the wing in relation to flight performance. In bat ecomorphology, the feeding and flight apparatus have been the subjects of much study; we direct our focus to these areas, recognizing that other aspects of morphology influence behavior and ecology and equally merit further study.

We emphasize several themes; the central role of body size as a determinant of mechanical and ecological function; the importance of recognizing ontogenetic, intersexual, and other intraspecific variation; the need for integrative analyses that span field and laboratory; and the role of computer modeling in present and future studies. We offer our views concerning what kinds of information are most likely to lead to new insights and effective integration of the work of morphologists and ecologists in the future.

Correlational Approaches to Assessing Form and Its Ecological Significance

Background

One basic and widely applied approach to ecomorphological analysis assesses aspects of organismal structure as well as its ecological attributes and seeks to describe patterns of interrelationship among them. Comparisons of this kind may take many forms, depending on the manner in which one characterizes form, function, and/or their interrelationship. Assessment of morphology can range from a simple description of one or a few characters to exhaustive characterization of shape. In some cases, investigators evaluate structure with no preconceived notions about the relative importance of particular features (e.g., Birch 1997; Bookstein 1997; Bookstein et al. 1985; Strauss and Altig 1992). These studies seek general descriptors that may capture some critical aspect of

form independent of functional analysis. Alternatively, theoretical or mechanical analyses and/or previous experimental studies may suggest that a given feature or suite of features are especially important.

Function or ecology may be quantified as categorizations of aspects of habitat, locomotion, food, and so on (e.g., Aldridge 1986b; Aldridge and Rautenbach 1987; Britton et al. 1997; Saunders and Barclay 1992). Studies of this kind then typically compare morphology and ecology among multiple taxa. Taxonomic sampling can focus specifically on phylogenetic lineages (e.g., Freeman 1981b; Saunders and Barclay 1992), sympatric communities (e.g., Bonaccorso 1979; Findley 1993), or dietary types (e.g., Fenton 1989, Norberg and Fenton 1988) or may seek to sample more broadly, even sampling the total diversity of bats (e.g., Norberg and Rayner 1987). Patterns of interrelationship among structural and ecological variables can then be described qualitatively or statistically.

Approaches that reveal patterns of correlation assess general patterns of relationship between morphology on the one hand and function or other ecological parameters on the other. Vaughan's (1959) research on wing anatomy and ecology in three bat species is one classic case in point. Analyses that extensively sample morphological and taxonomic diversity may reveal, for example, general associations among wing shape and habitat type (e.g., Findley et al. 1972; Norberg and Rayner 1987; Smith and Starrett 1979) or among robustness of jaws and types of foods eaten (Freeman 1981a, 1981b, 1998). These patterns, in and of themselves, give new insights into the relationship between structure and ecology. Additionally, patterns of strong correlation can be used to predict aspects of the ecology of rare or poorly studied taxa in those instances in which their anatomy is well described or is preserved in museum collections. These taxonomically comprehensive studies are particularly effective in identifying morphological and ecological extremes, in which relationships among form and ecology may be most readily described and interpreted. They also characterize subtle variation among more similar species. Correlational approaches can also generate specific and testable hypotheses that explore structural and behavioral relationships more deeply. Results of basic descriptive and correlational analyses are long-lived and can be revisited repeatedly as new approaches and data become available.

Critical Issues in Correlational Analysis

Body Size Relationships in Ecomorphological Studies

Body size dictates most aspects of organismal ecology and physiology (see Speakman and Thomas, this volume, Willig et al., this volume). It is shaped by intra- and interspecific interactions and by the physical environment (e.g., La Barbera 1986; 1989; Peters 1983; Schmidt-Nielsen 1984). In bats, body size influences flight behavior, diet selection, roosting, reproductive behavior and physiology, and virtually all other aspects of biology. Understanding patterns

of structure and behavior in relation to body size, then, is central to gaining an overall understanding of ecomorphology in the Chiroptera.

Numerous studies have demonstrated links among body size, basal metabolic rates, and the effectiveness of thermoregulation in mammals (Elgar and Harvey 1987; Hayssen 1984; Hayssen and Lacy 1985; McNab 1983,1990; Nagy 1987). Among bats, similar patterns have been suggested by several studies, as reviewed by Speakman and Thomas (this volume). For example, populations of one species of blossom bats (*Macroglossus minimus*) in New Guinea vary in body mass along an altitudinal gradient. These metabolically flexible tropical bats are significantly larger at lower elevations (16.4 g, vs. 15.3 g at higher altitudes), and the lower but not the higher altitude populations can readily enter torpor; the same is true for *Syconycteris australis* (16.3 g in lowlands and 15.3 g at higher elevation (Bonaccorso and McNab 1997). Cotterill (1998) found that in two sympatric African insectivorous bats the larger *Rhinolophus hildebrandi* has a longer prenatal development and a longer period of lactation than the smaller *R. simulator* (table 6.1). Because of the delayed but shortened embryonic development and shorter period of lactation in the latter species, pups are born closer to peak food availability in the wet season. However, body size interacts with many diverse influences on metabolic characteristics, including developmental patterns, life-history traits, environmental temperature variability, and diet. For example, *Melonycteris melanops*, the largest obligate nectarivore among bats (table 6.1), does not enter torpor at all body masses. As ongoing work extends studies to more species of diverse feeding habits and phylogenetic affinities, we may achieve a clearer view of the relative importance of body size as a determinant of metabolic traits.

Using body size to explain large-scale patterns in the ecomorphology of bats, Barclay and Brigham (1991) postulated that a combination of aerodynamic and sensory constraints limits body size in aerial insectivores. They proposed that increased body size decreases maneuverability and necessitates the detection of prey at greater distances. Hence, larger bats should employ relatively low-frequency echolocation pulses to reduce signal attenuation over long distances. As the frequency of echolocation signals decreases, however, the spatial resolution needed to detect small prey may be lost (see Jones and Rydell, this volume). The limited abundance of large prey, then, constrains dietary resources for large hawking bats (Barclay and Brigham 1991). This hypothesis has been tested in communities of insectivorous bats, and large species were found to take large prey, but small bats took only small food items (Aldridge and Rautenbach 1987, O'Neill and Taylor 1989). This positive relationship between body size and prey size is also consistent with Fenton's (1989) prediction that head length determines prey size for animal-eating bats. Additional evidence suggests that large, aerial insectivorous bats may not necessarily be limited to large prey. Aldridge and Rautenbach (1987) showed that large bats ate insects of a broad range of sizes and that there was a significant association between foraging habitat and the prey type. Consider-

Table 6.1. Body masses for species mentioned in text

Species	Body Mass (g) ^a
<i>Antrozous pallidus</i>	20.3
<i>Artibeus jamaicensis</i>	46.1
<i>Artibeus lituratus</i>	62.8
<i>Carollia</i>	10–25.0 ^b
<i>Carollia perspicillata</i>	18.6
<i>Carollia castanea</i>	14.7
<i>Corynorhinus townsendi</i>	9.9
<i>Desmodus rotundus</i>	35.2
<i>Eptesicus fuscus</i>	17.6
<i>Hipposideros commersoni</i>	91.4
<i>Lasiurus cinereus</i>	25.6 ^c
<i>Lasiurus borealis</i>	10.9
<i>Leptonycteris currosoae</i>	23.0
<i>Macroglossus minimus</i>	Lowlands 16.4
<i>Macroglossus minimus</i>	Highlands 15.3
<i>Melonycteris melanops</i>	53.3 ^d
<i>Myotis bechsteini</i>	8.4
<i>Myotis evotis</i>	4–11.0
<i>Myotis lucifugus</i>	7.9
<i>Myotis volans</i>	5–10.0
<i>Myotis yumanensis</i>	5.1
<i>Nyctalus noctula</i>	27.9
<i>Phyllostomus hastatus</i>	98.0
<i>Pipistrellus pipistrellus</i>	4.5
<i>Plecotus auritus</i>	7.5
<i>Pteronotus pamellii</i>	12–24.0
<i>Pteropus giganteus</i>	1175.0
<i>Pteropus poliocephalus</i>	800.0
<i>Pteropus scapulatus</i>	358.0
<i>Rhinolophus ferrumequinum</i>	19.0
<i>Rhinolophus hildebrandi</i>	25.4
<i>Rhinolophus simulator</i>	6.0
<i>Syconycteris australis</i>	Lowlands 16.3
<i>Syconycteris australis</i>	Highlands 15.3
<i>Tadarida brasiliensis</i>	13.5

^a Means or ranges derived from Silva and Downing (1995), from Freeman's unpublished database of diet in bats, and from references in text.

^b Adult range for *Carollia*.

^c Adult mass in non-Hawaiian *L. cinereus*.

^d *Melonycteris melanops* adults can range to 63 g.

ation of the relationship between body size and flight performance highlights the need to develop approaches that allow reliable, consistent assessments of maneuverability.

In evaluating relationships between aspects of body size and prey choice, assessing the validity of the hypothesis that small prey are unavailable to large bats calling at relatively low frequencies remains important. Recent work shows that the strength of echoes from insects is independent of the frequency of the echolocation pulse (Waters et al. 1995). *Nyctalus noctula*, a large aerial

insectivore (table 6.1), includes a substantial proportion of small dipterans in its diet (Jones 1995). Thus, body size may exert a broad influence on behavior and/or morphology of insectivorous bats that can be observed in large-scale, multi-species comparisons, but care must be exercised to isolate the effects of body size per se from those of other factors that may be correlated with body size to varying degrees.

Body size exerts a significant influence on foraging behavior in frugivores and nectarivores, as well as insectivores. Body size influences foraging behavior, albeit in somewhat different ways, in both frugivorous megachiropteran and phyllostomid microchiropteran lineages (Fleming 1993). Phyllostomids have relatively small foraging ranges, highly maneuverable flight, and highly selective diets; megachiropterans are typically less maneuverable, long-distance fliers, and dietary generalists. In phyllostomids, body size correlates with size of figs eaten, although large-bodied species will occasionally select small figs (Kalko et al. 1996). In contrast, there is no relationship between body size and size of fruit selected in megachiropteran frugivores (Dumont, this volume; Kalko et al. 1996). Body size also significantly influences diet and habitat use in bats that occur together in both wet and dry tropical communities in Costa Rica (Fleming 1991). Within the genus *Carollia*, as body size increases, the proportion of *Piper* fruits in the diet decreases, the proportion of large fruits in the diet increases, and time spent feeding decreases (table 6.1). In contrast, *Leptonycteris curasoae*, a large-bodied phyllostomid characterized by high wing loading, has wing morphology and foraging behavior convergent on that of megachiropterans (table 6.1). Unlike most phyllostomids that forage in mesic habitats, it traverses long distances across arid or semiarid environments to feed on flowers and fruits of three species of columnar cacti (Fleming 1993; Fleming and Eby, this volume, Sahley et al. 1993).

Richards (1995) teased out subtle results regarding body size and diet in 13 species of Australian megachiropterans. He grouped species into five feeding categories and found that there were large (>300 g) and small (<60 g) fruit and nectar specialists but only large-bodied generalists (table 6.1). Each group contains both an abundant species and one or more rare species. *Pteropus scapulatus*, with its reduced dentition, is indeed a specialized nectarivore (Freeman 1995). The large nectarivorous species are highly mobile and have wide distributions correlated with the distribution and diversity of eucalyptus. They are highly sensitive to olfactory cues and can respond quickly to mass flowering. These discoveries have implications for coevolution of bats and native forests and for the conservation of both (see Racey and Entwistle, this volume).

Intraspecific Patterns in Ecomorphological Studies

An important element in ecomorphological thinking is the recognition that if interspecific morphological variation is associated with variation in behavior

and ecology, then morphological variation within species might also have behavioral consequences. For example, wing morphology varies not only with body size but also between sexes and among developmental stages within single species. This variation influences wing loading, aspect ratio, and mass distribution, which, in turn, affect flight performance characteristics such as turning ability, speed, and metabolic cost (e.g., Adams 1996, 1997; Hughes et al. 1989, 1995; Jones and Kokurewicz 1994). For example, wing loading in developing horseshoe bats, *Rhinolophus ferrumequinum*, decreases with age as length of the hand wing increases disproportionately relative to length of the arm wing. Ontogenetic change in the relative lengths of these two regions of the wing can thus modify flight efficiency with age (Hughes et al. 1995). As wing development progresses in *Pipistrellus pipistrellus*, wingbeat frequency decreases. This basic shift in flight kinematics may be driven by ontogenetic changes in wing moment of inertia as animals mature and increase in body mass and by the maturation of wing musculature (Hughes et al. 1989).

Ontogenetic variation in wing shape in *Myotis lucifugus* also appears to be ecologically significant (Adams 1996, 1997). During postnatal growth, as wing size increases, aspect ratio increases and wing loading decreases; simultaneously, growing bats forage in increasingly cluttered habitats. Interestingly, adult bats forage in a variety of habitats but shift to more cluttered habitats when juveniles became volant. Fecal samples also show a shift in diet with age, suggesting that adults may selectively limit competition with juveniles (Adams 1997). In this species, the greatly varying rates of muscle development may also be functionally or ecologically significant; the primary postural muscles of the hind limb are more mature at birth and reach adult fiber-type characteristics far more rapidly than do flight muscles (Powers et al. 1991).

In female bats, wing loading and flight kinematics can also vary with reproductive condition. For example, in *Phyllostomus hastatus*, a large phyllostomid, wing loading changes with seasonal changes in body mass in females (Stern et al. 1997; table 6.1). Wing loading and body mass also change in *Pipistrellus pipistrellus* in different reproductive conditions, and the highest wing loadings are seen in pregnant females (Webb et al. 1992). Lactating female *P. pipistrellus* that may be under metabolic stress and/or may have lower mass than nonreproductive females had lower wingbeat frequencies than either pregnant or postlactating bats (Hughes and Rayner 1993). These findings may have important implications for habitat use and prey selection, especially if pregnant females switch to less maneuverable prey types (Aldridge and Brigham 1988) or if power requirements for flight increase during pregnancy, as one might expect when wing loading increases (Hughes and Rayner 1991, 1993).

Kalcounis and Brigham (1995) found that wing loading was a significant predictor of habitat use by *Myotis lucifugus*, regardless of age or reproductive status. Individuals with higher wing loading foraged in less cluttered habitat,

suggesting that wing loading rather than dietary needs imposed by reproductive condition constrained foraging behavior. In *Myotis yumanensis*, Brigham et al. (1992) found no intraspecific differences in diet or habitat use among four reproductive and age classes. Clearly, we have only begun to assess the degree to which intraspecific morphological variation relates to ecology; this subject certainly merits further study.

Case Studies

Contemporary researchers have contributed to our understanding of the complex patterns of interrelationship among ecological and morphological characteristics of bats. These analyses have elucidated many anatomical systems in numerous taxa and continue to provide the primary data for broad generalizations. Here, we select two groups of analyses that illustrate some of the diversity of current study of bat ecomorphology. These case studies represent only a small fraction of the ongoing work in this area but highlight the kinds of results that derive from this approach.

Specialization of the Musculoskeletal System of the Desmodontine Hind Limb

It has long been recognized that the dimensions of bones vary in relationship to body size (Alexander et al. 1979; Galilei 1637; McMahon 1973; Schmidt-Nielsen 1984). Among mammals, and among subgroupings within mammals, linear dimensions such as length and diameter of the long bones typically change in proportion to $(\text{body mass})^{0.33}$ (e.g., Biknevicius 1993; Demes and Jungers 1993; Alexander et al. 1979). Given that body mass is proportional to body volume, in turn a function of linear dimensions to the third power, these results demonstrate that, by and large, the shape of bones changes little in relation to body size, a pattern often designated as geometric similarity or isometry (Swartz and Biewener 1992). General patterns of scaling can serve as background descriptions against which specializations of bone shape deviations can be discerned.

Within bats, the dimensions of the long bones of the limbs generally demonstrate geometric similarity, but bats are distinctive in comparison to nonvolant mammals in several ways (Swartz 1997, 1998). If the evolution of flight is associated with reduced mechanical importance of the hind limbs for quadrupedal locomotion, and if the construction and transport of bone tissue requires a significant input of metabolic or nutritional resources, we predict that selection will favor reduction in mass of the hind limb skeleton. Indeed, hind limb bones of bats are clearly reduced in size and strength in comparison to those of nonvolant mammals (Howell and Pyka 1977; Swartz 1997, 1998; fig. 6.1). Along with this morphological specialization for the ecology of flight, bats and their closest gliding relatives have acquired distinctive specializations of the tendons and tendon sheaths of the digits of the foot (Bennett 1993;

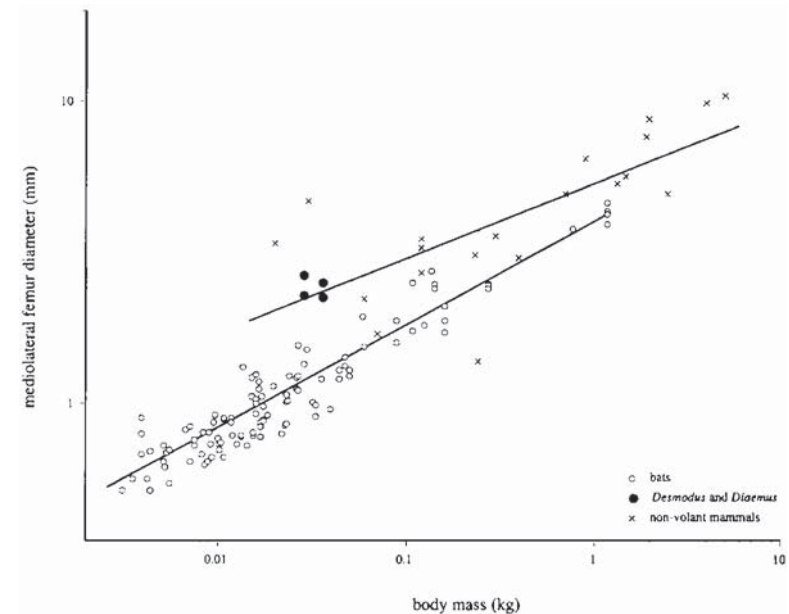


Figure 6.1. Log-log plot of femur diameter versus body mass of diverse bats and related and/or similarly sized nonvolant mammals. Vampire bats clearly cluster with nonvolant mammals and are distinctive in relation to bats of their body mass. The great robusticity of the desmodontine femur is likely related to their distinctive pattern of terrestrial locomotion (modified from Swartz 1997).

Quinn and Baumel 1993; Schutt 1993; Simmons and Quinn 1994). Structural modifications of adjacent surfaces of the long digital flexor tendons and their sheaths produce a ratchet-like, passive locking mechanism that may reduce or eliminate the need for activity in foot musculature in hanging postures. This interlocking of tendons and their sheaths, however, likely reduces the capacity for rapid ankle and toe flexion and extension.

The vampire bats, genera *Desmodus*, *Diaemus*, and *Diphylla*, composing the subfamily Desmodontinae, differ from all other bats in the structure of the hind limb and in their highly specialized feeding ecology (Schutt 1998). To approach and contact warm-blooded prey without detection, blood-feeding bats employ locomotor behaviors that are unusual in bats, moving stealthily across the ground and/or climbing rapidly. The evolution of this lineage clearly involved a fundamental ecological shift that has profoundly altered the mechanical demands placed on the hind limb. Terrestrial or arboreal locomotion, in contrast to flight, favor hind limb morphology in which digital tendons

can slide freely in their sheaths throughout a large range of motion and in which the structural strength of the hind limb bones is increased relative to that of other bats. Indeed, recent work has directly documented the large forces experienced by the hind limbs of vampire bats during jumping (Schutt et al. 1997). Thus, although bats are unique among nonaquatic mammals in the degree of reduction of the hind limb bones, desmodontines alone among bats have reversed this trend and are distinctly characterized by remarkably robust femora and tibiae (fig. 6. 1), and the loss of the characteristic bat digital foot tendon-locking mechanism (Howell and Pylka 1977; Schutt 1993; Swartz 1997).

Chiropteran Craniodental Structure and Feeding Ecology

Bats exploit a wider range of food types than any other mammalian order. Teeth and jaws are the morphological locus of direct interaction with food, and the relationship between dietary diversity and craniodental structure has been the subject of a series of ecomorphological analyses (e.g., Dumont 1997a, 1997b, 1999; Freeman 1979, 1981a, 1981b, 1984, 1988, 1992, 1995, 1998, 2000). Studies of many species from diverse dietary and taxonomic groups have focused on a variety of components of the skull and dentition. Amid the great structural diversity in the teeth and jaws of bats, this approach has uncovered a number of important generalizations.

The structure of the teeth and their skeletal supports are relatively consistent among insectivorous bats but are distinctive in groups that have more specialized diets. For example, carnivorous phyllostomids, megadermatids, and nycterids have undergone evolutionary transitions from eating "a hard-covered package with soft insides [insects, especially beetles] to eating a soft-covered package with hard insides [vertebrates]" (Freeman, 1984). This distinctive feeding ecology, independently evolved several times, is correlated with a suite of morphological specializations. Carnivorous bats possess an elongated metastylar ridge on the upper molars and an enlargement of the reciprocally interlocking protoconids. These features have long been recognized as correlates of flesh eating and the ability to slice rather than crush food items in diverse mammalian groups. Carnivorous bats also possess lower molars with small talonid areas, relative to trigonid areas, and a relatively increased total area of the upper molar row. Both may be features related to improved slicing at the expense of crushing effectiveness (Freeman 1998, 2000). Carnivorous bats also possess relatively thin mandibles, large brains, large pinnae, negatively tilted basicranial axes, and large body mass in comparison to their purely insectivorous relatives (Freeman 1984; fig. 6.2). The morphological pattern observed in carnivorous species is also observed to lesser degrees among insectivorous bats that eat primarily soft-bodied insects, for example, moths, in contrast to those that specialize on relatively hard or tough prey, for example, beetles (Freeman 1979, 1981a). Bats that eat tough prey often

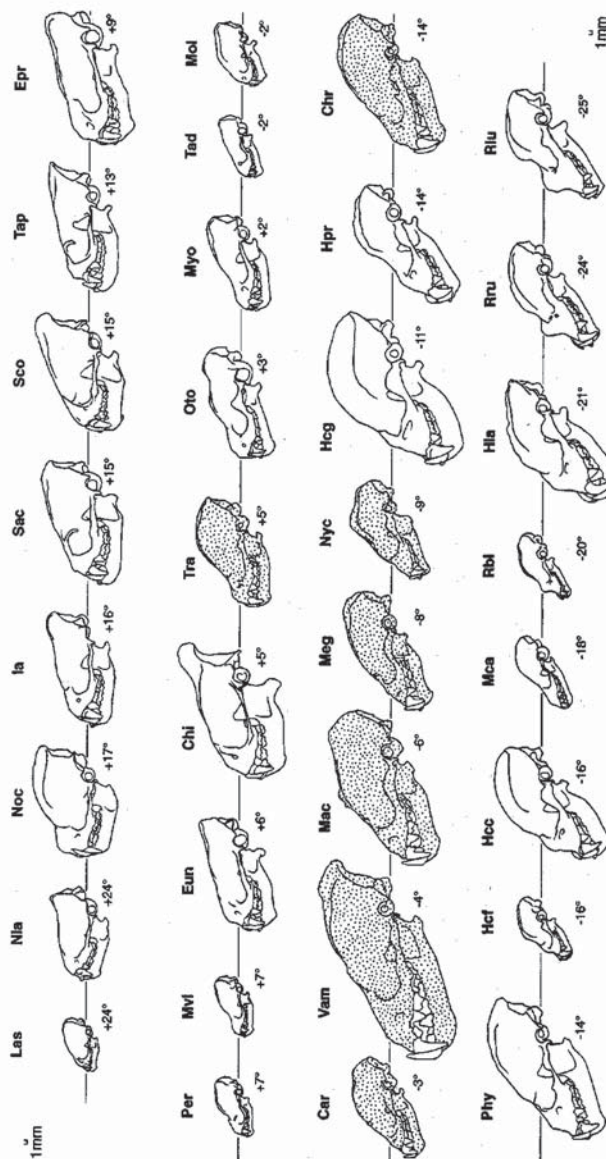


Figure 6.2. Bats are arranged so that the skull's basicranial axis is aligned horizontally (modified from Freeman 1984). Oral emitting bats have a positive or only slightly negative tilt of the head, and nasal-emitting bats have a negative tilt. Carnivorous bats from three families are shaded. *Trachops* may not be an obligate carnivore (Freeman 1984). Abbreviations of species are alphabetic within phylogenetic family order: *Peropithecus kappleri* (Per), *Saccolaimus peli* (Sac), *Taphozous nudicastris* (Tap); *Nyctarctis grandis* (Nyc); *Nyctarctis grandis* (Nyc); *Carollia* spp. (Car), *Macrotus* spp. (Mac), *Megaderma* spp. (Meg); *Rhinolophus blasii* (Rbl), *R. luctus* (Rlu), *R. trifidus* (Rru); *Hipposideros c. commersoni* (Hcc), *H. c. gigas* (Hcg), *H. lankaditza* (Hla), *H. pratti* (Hpr), *H. ruber* (= *H. caffer*, Hcf); *Noctilio leporinus* (Noc), *Chrotopterus auritus* (Chr), *Macrotus californicus* (Mac), *Phyllostomus hastatus* (Phy), *Trachops cirrhosus* (Tra), *Vampyrum spectrum* (Vam); *Ia io* (Ia), *Lasiurus borealis* (Las), *Myotis myotis* (Myo), *M. velifer* (Mvi), *Nyctalus lasiops* (Nla), *Scotophilus nigrita gigas* (Sco); *Chetronomus torquatus* (Chr), *Eumops perotis* (Epr), *E. underwoodi* (Eun), *Molossus molossus* (Mol), *Otomops martiensseni* (Oto), and *Tadarida brasiliensis* (Tad).

have robust skulls with thick dentaries, elongated canines, and short, wide faces (fig. 6. 3).

Skulls of oral-emitting insectivorous bats that eat tough prey show a convergence toward felids and hyaenids (Freeman 1984, 2000). These independent lineages share short, wide faces that bring the canines close to the fulcrum of the jaw and allow increased volume of the masseter muscle and, in some cases, the temporalis as well; the two large jaw-closing muscles are the primary determinants of bite force magnitude. In contrast, the nasal-emitting beetle specialist, *Hipposideros commersoni*, has a vertically expanded but thin dentary and taller sagittal crest that expands the skull vertically but not in breadth (Freeman 2000; fig. 6.3).

Fruit-eating microchiropteran bats have wide palates and faces—associated, potentially, with the ability to remove large chunks effectively from relatively large fruits and/or the ability to transport large fruits—and small stylar shelf areas that create a rim on the labial aspect of basin-like molars (Freeman 1988). Rimming the molars produces an efficient cutting edge that surrounds the entire perimeter of palate, with the rim of the flattened lower molars nesting inside that of the upper teeth (Freeman 1988). Molars with shallow basins surrounded by a rim are also typical of other mammalian frugivores, particularly megachiropterans, marsupials, and primates (Freeman 1988, 1995, Lucas 1979; Rosenberger and Kinzey 1976; Slaughter 1970). Relatively flat molars in the rear of the mouth of frugivores crush in a mortar-and-pestle-like arrangement; rims on the lower molars make up the “pestles” that are driven into the basins interior to the surrounding rim on the upper molars to shear as “mortars.” In this way, bats extract nutritious juice and separate it from nonnutritive pulp or indigestible seeds (Freeman 1988, Lucas and Luke 1984).

The most derived phyllostomid frugivores have small canines, possibly related to burying the face in the fruit and not having to transport fruit (e.g., *Centurio senex*). Other micro- and megachiropteran frugivores have longer canines that are likely useful in gripping fruit during transport (Freeman 1988). Frugivorous bats also differ from non-fruit-eating species by possessing greater tooth area in the anterior part of the tooth row. In contrast, more omnivorous bats have more equal allocation of occlusal area among the different kinds of teeth (Freeman 1988, 1998, 2000).

Employing a functional perspective to understand and interpret tooth and skull design of frugivores is not a trivial exercise. Fruits are a very broad class of food items and may vary substantially in the mechanical challenges they present to the feeding apparatus. The outside covering may be tough or brittle, soft or hard, and the inside of the fruit can range between hard and extremely soft, sometimes even in a single species, depending on the degree of ripeness (see Dumont, this volume). Overall fruit size relative to animal’s jaw apparatus is also critical. Although it may be most appropriate botanically to

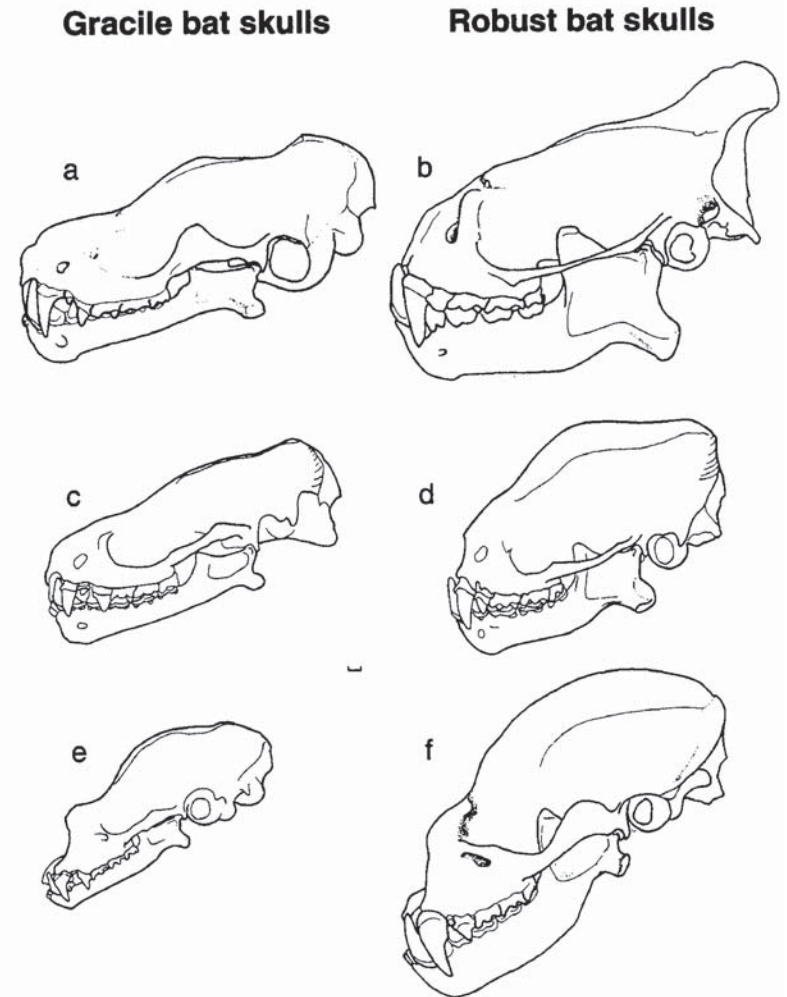


Figure 6.3. Bat skulls on the left are delicately built or gracile, and ones on the right are robust. Robust skulls have large cranial crests, fewer but larger teeth, and thicker dentaries (Freeman 1979, 1981a). Robustness or lack thereof is likely, in part, mediated by softness or hardness of items in the diet. *a*, *Otomops martiensseni*, an Old World molossid bat, has one of the most gracile skulls in its family. Recent data indicate it is a moth specialist (Rydell and Yalden 1997). *b*, *Cheiromeles torquatus*, an Old World bat and robust extreme, eats harder prey, such as grasshoppers and beetles (Freeman 1979, 1981b). *c*, *Nyctinomops macrotis*, a New World molossid with an extreme gracile skull, is a moth specialist (Freeman 1979, 1981a). *d*, *Molossus ater* is a New World molossid with an extreme skull that eats harder items, such as beetles (Freeman 1979, 1981a). *e*, *Rhinolophus blasii* is a known moth specialist (Freeman 1981a). *f*, *Hipposideros commersoni* is a known beetle specialist (Vaughan 1977).

classify fruits taxonomically or by their morphology (i.e., drupes, berries, pomes, aggregate and multiple fruits), these classification schemes are far less relevant to the frugivore than the size and mechanical nature of the fruit (Dumont 1999, this volume; Freeman 1988; Lucas 1979; Lucas and Luke 1984). Just as the ecology of nectar- and pollen-feeding bats is distinctive, so is their craniodental morphology. These taxa possess, to varying degrees, elongate, narrow rostra and greatly reduced postcanine teeth, although the degree to which these specializations are seen differs between microchiropteran and megachiropteran nectarivores (Freeman 1995). Nectarivore canines remain relatively large, perhaps for structural support as the tongue works to obtain nectar. In mammals other than bats, dental reduction is most common among insectivorous, particularly ant-eating, taxa, in which the tongue has taken on a central role in food processing. Similarly, the tongues of nectar-feeding bats appear to play a central role in food acquisition and processing and are as specialized in their morphology as the mineralized portions of the feeding apparatus (Griffiths 1982). Secondarily, the distinctive skull and palate shape in chiropteran nectarivores necessarily limits the attachment area and available space for jaw musculature. This reorganization of musculature may be associated with a substantial reduction in the magnitude of bite forces these species can generate; however, the function of the enlarged canines, which are long and sharp, has yet to be explored in species that specialize on nectar and pollen.

From a broad comparative perspective, species within nine microchiropteran families (Phyllostomidae, Molossidae, Vespertilionidae, Emballonuridae, Rhinolophidae, Megadermatidae, Nycteridae, Noctilionidae, and Mormoopidae) are unevenly distributed throughout the relatively large morphospace representing ecologically significant craniodental features (Freeman 2000; figs. 6.3 and 6.4). Insectivorous and carnivorous bats from many lineages fall within a circumscribed area that can be designated as "insectivore morphospace." However, although numerous phyllostomids have retained insectivory and its associated morphologies, four unique feeding ecologies have evolved from the primitive insectivorous condition within this group. Concomitantly, four divergent suites of morphological specializations appear within subgroups of this diverse family (fig. 6.4). Within the Vampyrinae, a tendency toward increased carnivory is associated with changes in tooth form and an increase in the size of the teeth relative to the palate and appears, secondarily, to have facilitated the evolution of increased body size (Freeman 1984, 1988, 2000). Within the Glossophaginae, nectarivory is associated with rostral lengthening, reduction of tooth size relative to the palate, and specialization of the structure and function of the tongue (Freeman 1995, 1998, 2000; Griffiths 1982). Many bats in the Stenodermatinae possess shortened rostra and diverse patterns of loss of the insectivorous dilambdodont molar morphology and pursue a primarily fruit-eating ecology (Freeman 1988, 1998,

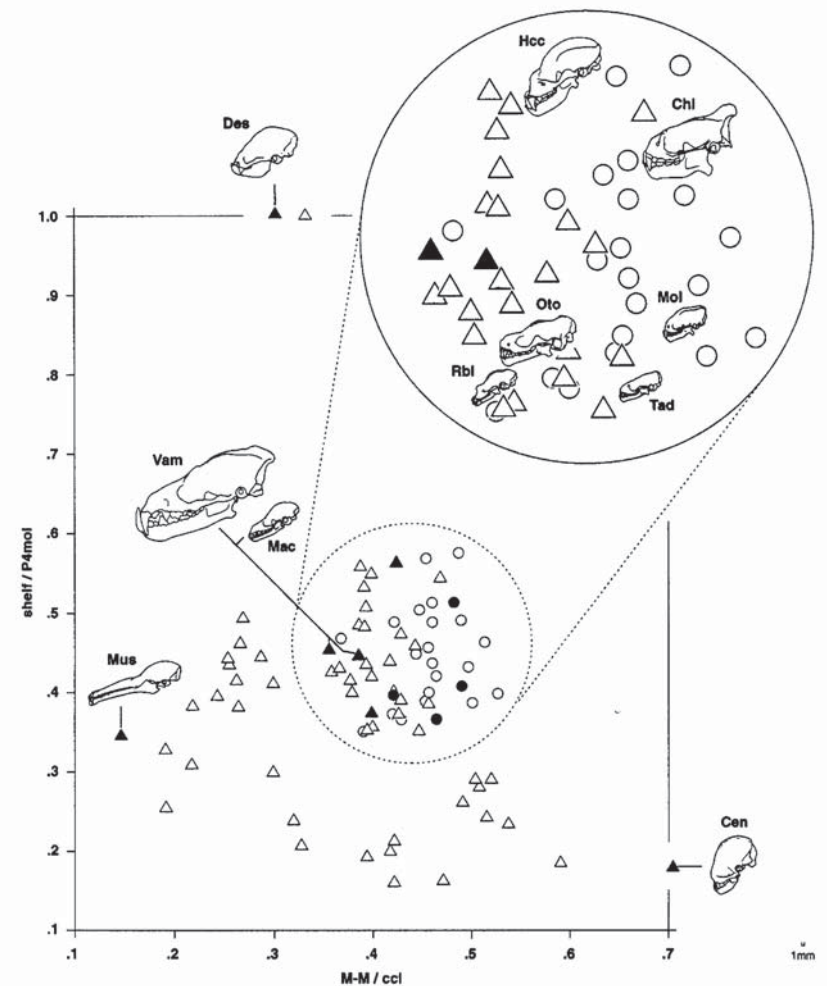


Figure 6.4. Bivariate plot of the relative area of the styler shelf on the upper molariform tooth row (shelf/P4mol) versus breadth of the palate at the molars relative to the length of skull (M-M/ccl) showing the comparative scatter of insectivorous species from nine microchiropteran families (encircled) and phyllostomids, which fall largely outside the circle (modified from Freeman 2000). Diversity in Phyllostomidae is greater than that of all other families put together. Circles represent oral emitters and triangles, nasal emitters. Skull profiles in the insert replace the filled symbols on the graph. Diversity of insectivores within the circle includes large and small, oral and nasal emitters, and bats with robust and gracile skulls. Most bats from figure 6.3 are included for comparison of diversity within insectivorous bats (*Rhinolophus blasii* [Rbl], *Otomops martiensseni* [Oto], and *Tadarida brasiliensis* [Tad] are gracile; and *Hipposideros c. commersoni* [Hcc], *Cheiromeles torquatus* [Chi], and *Molossus molossus* [Mol] are robust). Extreme phyllostomids are pictured for comparison of diversity among Microchiroptera (*Musonycteris harrisoni* [Mus], a long-faced nectarivore; *Centurio senex* [Cen], a short-faced frugivore; *Desmodus rotundus* [Des], a sanguinivore; *Macrotus californicus* [Mac], a small-sized insectivore; and *Vampyrum spectrum* [Vam], a carnivorous giant).

2000). In association with the evolution of blood feeding, the Desmodontinae display reduction of many elements of the dentition.

The phyllostomid pattern of interrelationships among feeding ecology and morphology of the teeth and jaws may shed light on ecological patterns at higher levels and contribute to a better understanding of bat community ecology in Neotropical forests (Freeman 2000). The evolutionary acquisition of novel feeding modes appears to have influenced not only the range of phyllostomid diversity but also the structure of bat assemblages (Patterson et al., this volume). Although non-insectivorous phyllostomids make up only approximately 40% of the bat species diversity in La Selva in Costa Rica and Barro Colorado Island in Panama, four genera—*Glossophaga*, *Sturnira*, *Carollia*, and *Artibeus*—account for between 86% and 89% of bat biomass, respectively (Freeman 2000 from data in Bonaccorso 1979; La Val and Pitch 1977; Timm et al. 1989). Future studies may be able to gain deeper insight into the interspecific interactions that determine this pattern and help to provide a clear causal linkage between morphological novelty in the feeding apparatus and ecological and evolutionary success.

Challenges to Correlational Analyses: Some Caveats and Limitations

Correlational approaches provide meaningful insight into the ecological significance of patterns of morphological variation, but the power of these approaches depends on a number of factors. Ideally, morphological and ecological variables employed in ecomorphological analyses are causally related. However, given our limited understanding of biological complexity, we face a significant probability of spurious results, and therefore, sometimes it may be virtually impossible to link conclusively the morphology in question to the ecological parameters of interest. Organismal morphology is highly integrated (e.g., Voss et al. 1990; Shubin and Wake 1996), and the characters of interest to us in ecomorphological studies are rarely if ever discrete, autonomous features controlled independently by the genetic system, free of covariation with characters unrelated to the function or ecological attribute under study. Changes in one part of an organism's structure necessarily bring at least some correlated changes, seriously confounding ecomorphological analysis. Independent of genetic correlations, there may be correlations among structural features because of morphological or physiological requirements not related to those aspects of ecology that are the foci of a particular analysis. To reveal causal links between structure and function, investigators must therefore sometimes employ additional, noncorrelational approaches. The more direct the connection between morphology and function, the greater the investigator's ability to discern important aspects of ecomorphology and avoid misleading correlations. Moreover, in some cases, very small differences in morphology can profoundly affect function and, in others, even relatively

large morphological divergence may have little functional or ecological significance.

Correlational approaches to ecomorphology also depend critically on the characterization of the relevant ecology. For example, analysis of the relationship between craniodental structures and feeding ecology requires dietary description. But, by virtue of availability or choice, the type of food processed by the jaws and teeth may vary from year to year and from season to season in any given year and, in species with multiple feeding bouts in a single night, depending on the time of night. Within a single species characterized by a particular morphology, there may also be considerable geographic variation in diet. "Menus" at different times may have vastly different mechanical properties and thus impose disparate demands on the feeding apparatus. Patterns of correlation among craniodental characteristics and diet may be meaningful only when one considers the entire dietary repertoire of the species of interest, rather than predominant or preferred food items.

Recent research emphasizes the need for detailed fieldwork to obtain a realistic and biologically meaningful view of a species' diet. To obtain a clear picture of relationships among diet and morphology, sampling effort, prey availability, nightly, seasonal, and even year-to-year, variation must be taken into account. For example, lactating females of *Tadarida brasiliensis* employ two distinctive feeding pulses: a bout between early evening and midnight and an early morning bout (Whitaker et al. 1996). During the first bout, these bats fed largely on beetles and lygaed bugs, prey of relatively high strength and toughness, and in the early morning, most prey were soft-bodied and more easily processed moths. Clearly, if dietary data were collected from only one of these feeding bouts, the reliability of patterns of correlation between this species' morphology and feeding ecology would be limited.

Bats can take advantage of seasonally abundant prey and may opportunistically select prey at high densities (Brigham et al. 1992; Jones 1995; Waters et al. 1995). Under these conditions, animals may forage in habitats not predicted by the general patterns of relationship between wing morphology and flight mode. For example, frugivorous phyllostomid species such as *Artibeus lituratus* or *A. jamaicensis* may take advantage of seasonal nectar resources at flowering trees (Handley et al. 1991), although they lack the small body size and relatively low wing loading, high wing aspect ratio, and long wing tips often seen in insectivorous phyllostomids (Norberg and Rayner 1987; table 6.1). In insectivorous bats, it may be especially difficult to establish a clear relationship between flight morphology and diet when it is necessary to rely on indirect analysis of feeding ecology. Fecal analysis or examination of culled insect parts may not reliably indicate whether prey have been captured in midair or gleaned from a substrate.

Variation in diet for a given species is also important over longer timescales

and over its geographical distribution. Indeed, it may be the foods eaten in times of extreme environmental or population stress that exert the greatest selection pressures and are therefore most critical for determining morphological structure (Grant 1986; Grant and Grant 1989). Studies of the feeding ecology of *Lasiurus cinereus* in New Mexico show that this species has strong preferences for soft-bodied moths. However, in Canada, at the height of the insect season, odonates, beetles, and other hard prey dominate its diet (Barclay 1985). Further, changing distributions of prey or fruit abundance can influence bat diets directly or in more subtle ways, through interactions among consumers of local food items. Competition among sympatric species for specific foods will change from year to year in association with changes in population I structure of either prey or predator species. For example, dietary overlap between *L. cinereus* and *L. borealis* varies from year to year, with the greatest overlap in a year of minimum food abundance (Hickey et al. 1996).

Limited knowledge of the full range of food items for a species can, in such instances, have a large impact on our ability to relate ecology to structure. Based on morphology of the skull and teeth, in the absence of dietary evidence, Freeman (1981a) suggested that *L. cinereus* should be readily able to consume hard prey such as beetles. This apparent mismatch of structure and function might well contribute to a view that the relationship between feeding performance and craniodental morphology is not always strong. But how closely the morphology of the *Lasiurus* feeding apparatus relates to diet depends on whether one considers the southern or northern populations. The more complete picture of the diet in this species suggests that the ability to process hard prey is, at least periodically, a critical functional element of its skull and dentition.

Analyses of fecal or stomach contents must account for the timing and/or geography of sample collection to avoid misleading interpretations. To date, however, there are few species for which we have chronicled dietary information in sufficient detail to address these diel, seasonal, annual, and geographic variations. Some of the most comprehensive studies of dietary variation have been carried out on endangered temperate species (Best et al. 1997; Lacki et al. 1995; Sample and Whitmore 1993). Such analyses consistently demonstrate hourly, daily, and seasonal variation in dietary composition and often show that distribution of prey types differs significantly from their availability in the environment. For tropical bats, seasonal changes often mean dramatic dietary changes; these remain largely undocumented. As a consequence, inferences concerning diet based on distribution of available resources may not accurately reflect the diet of a given species.

In general, correlational analyses are most meaningful when specific confounding factors are identified. In particular, virtually all aspects of organismal form and behavior are strongly affected by the overall size of the organism; thus, comparisons among taxa require explicit consideration of the effects

of body size. Likewise, it is well established that groups of species may share certain morphologies or behaviors by virtue of their inheritance from a common ancestor instead of through the selective pressures imposed by the contemporary ecological setting. It is thus necessary to account for the effects of phylogenetic relationship to discern ecomorphological patterning (e.g., Felsenstein 1985; Garland et al. 1999; Losos 1996; Losos and Miles 1994; Perry 1999; see below, "Phylogenetic Considerations in Ecomorphology").

Comparative/correlational approaches have produced the core of our understanding of the relationships between morphology and ecology of bats. Through research over the past several decades, broad, general patterns of structure/function relationship have emerged (e.g., Aldridge and Rautenbach 1987; Findley 1993; Freeman 1998; Norberg and Rayner 1987). Finer-scale patterns have also been uncovered, particularly within relatively diverse and speciose genera or families (e.g., Findley [1972] for *Myotis*, and Freeman [1981b] for *Molossidae*). This approach simultaneously improves our understanding of the meaning of structural diversity and points to new directions for functional morphological and ecological research. Strong patterns of correlation among ecological and morphological features can be used to generate robust hypotheses about function or ecology for species about which little is known. In species accessible to further ecological study, these predictions can, ultimately, be tested by new data, further refuting our understanding of the basic ecomorphological relationships.

Of equal importance, deviations from robust patterns can be identified. "Outliers" from otherwise highly regular patterns can direct our attention to interesting and important biological phenomena and/or point to critical features of the structure or ecology of the group that have been underappreciated or ignored. Discovery of patterns and deviations from these patterns describe diversity and generate hypotheses that can then be further developed and tested in the field or laboratory.

Function-Focused Approaches to Morphological Analysis

Ecomorphological analysis builds on the rich databases of observations of field ecology and comparative morphology and on the interpretations of these data within their primary disciplinary contexts. Correlative comparative approaches identify patterns of covariation among ecological and morphological characteristics of organisms by synthesizing diverse primary data; to further interpret these patterns, physiological and experimental approaches can often explore why particular aspects of morphology relate to certain ecological characteristics. Explicitly functional analyses can also offer opportunities to confirm that proposed relationships of structure to ecology are biologically critical and to distinguish causation from secondary correlations.

Probing causal relationships between organismal design and behavioral

performance may require that one quantify morphology and/or performance in a very specific manner. This approach often requires analysis of how design controls or constrains behavior. A focus on the biological roles of specific structures, and on how multiple structures interact in a functioning whole, may be particularly well suited to achieving the goals of ecomorphological analysis.

Morphologists can choose general descriptors of organismal structure by attention to those aspects of morphology most likely to affect performance. For example, even in the absence of a detailed understanding of the aerodynamics of flapping flight of bats, one can feel confident that wing size and shape influence flight performance in some way and that skull form does not. However, this intuitive approach can sometimes be imprecise or misleading, particularly when comparisons are made among taxa of differing body sizes. Some functional parameters change as linear functions of body mass, and some as various power functions; hence functional equivalence at differing body sizes may require substantial modifications of structural design (Koehl 1995; LaBarbera 1989; McMahon 1984; Schmidt-Nielsen 1984). Conversely, similar shape at differing body sizes often implies differences in performance capabilities.

Even when structural descriptors are based on biomechanical analyses, function cannot be inferred unambiguously from morphology alone. No functional analysis can encompass all relevant structural and physiological complexity, and a number of critical variables in all real-world functional analyses are estimated, not measured directly. We illustrate this by considering the analysis of the form of a muscle that one believes is functionally important to a particular behavior.

The mass of a given muscle, or interspecific variation in mass, are often construed as indicative of functional and mechanical importance. However, it is not mass but physiological cross-sectional area and three-dimensional anatomical location relative to bony levers and joints that are required to estimate the largest force a muscle could produce under maximal stimulation and for a particular posture (Gans 1982). The internal architecture of the muscle, including its fiber length, degree of pinnation, and location of its origin and insertion, provide better guides to a muscle's functional potential than its size. Moreover, the intensity with which a muscle is activated and the timing of the onset and offset of muscle contraction with respect to a particular activity cannot be predicted a priori and often are not consistent with classic descriptions of muscle function based on anatomy alone. What appears to be a flexor, as determined by anatomical location, may remain electrically silent during primary flexing motions of the joint it crosses and instead may generate significant forces only during controlled extension. The positions of bones at a joint, and thus a muscle's leverage, also change continuously during movement (e.g., Loeb and Gans 1986). Moreover, multiple muscles that may act

either synergistically or antagonistically to the muscle of interest cross many joints. Hence, a particular motion generated by the application of a specific force moment about a joint can be achieved by a virtually infinite number of combinations of force magnitudes contributed by each of the anatomically relevant muscles.

Although direct measurement of muscle activity patterns, or electromyography (EMG), presents considerable technical challenges, this technique provides invaluable information that can contribute directly to the interpretation of musculoskeletal anatomy. Recently, numerous studies have employed electromyography to assess directly the timing and relative intensity of muscle activity during particular movements in humans and a great diversity of animals, including bats (e.g., Altenbach and Hermanson 1987; De Guedre and De Vree 1984, 1988, 1990; Hermanson and Altenbach 1981; Lancaster et al. 1995). These analyses can be employed to develop an understanding of how muscle activation patterns vary among behaviors. For example, the pectoralis muscle of *Artibeus jamaicensis*, *Antrozous pallidus*, and *Eptesicus fuscus* does not simply adduct the wings during the downstroke. Instead, during slow flight, the pectoralis is activated midway through the upstroke and ceases activity before the mid-downstroke (Altenbach and Hermanson 1987).

Electromyography, like other experimental methods, including in vivo bone strain measurement (Biewener 1992; Swartz 1991, 1998; Swartz et al. 1992) and force platform analysis (Schutt et al. 1997), requires detailed information concerning movements of specific anatomical structures during the behaviors of interest; this kind of information is also extremely informative in and of itself. In addition, outputs of many functional analyses are very sensitive to aspects of kinematics. This is particularly true in analyses of flight because of the complex, nonlinear nature of aerodynamic forces and flight energetics. Photographic methods, particularly multicamera, short-exposure still photography, and high-speed cinematography and videography provide considerable insight into mechanically and aerodynamically important aspects of the three-dimensional conformation of wings (Aldridge 1986a, 1987; Altenbach 1979; Norberg 1970, 1972, 1976a, 1976b, 1976c; Rayner et al. 1986). For example, recognition of multiple distinctive kinematic patterns or gaits in bat flight required accurate records of multiple wing landmarks over a range of flight speeds (Aldridge 1986a, 1986b; Norberg 1976a, 1976b, 1976c; Rayner 1986). Visualization techniques can, ultimately, provide information that is critical to functional interpretations of morphology, and fortunately, it is increasingly possible to attain high resolution, high-speed sequences at relatively low cost. Imaging equipment for low light environments and compact, portable instrumentation will also greatly expand opportunities to see and record flight and feeding behaviors in great detail, both in the field and in the lab.

The techniques of direct functional study all share certain limitations. They

are typically time, labor, and equipment intensive, and necessitate that investigators have access to live animals in relatively controlled laboratory conditions. These features constrain sample sizes and restrict the number of taxa that can be studied. However, direct functional study of a limited nature can serve as a key intermediate step in analysis that can thereafter guide the selection of measurements that can be made more easily from large numbers of individuals and/or species.

Experimental Approaches to Understanding Ecomorphology of the Feeding Apparatus

Coupled with ecological data, measures of functional performance can provide important insight into the constraints that affect behavior in the wild. To understand the functional role of a particular morphology requires that one identify the mechanisms behind correlations between morphological traits and behavior. In studies of tooth morphology and diet in bats, experimental studies that examine the mechanical limitations of tooth and jaw morphology with respect to the mechanical properties of prey are crucial to establishing a link between morphology and diet (see Dumont, this volume). The physical nature of food provides a selective influence on the shapes and configurations of the teeth (Lucas 1979). Experimental approaches that identify how the morphology of particular elements of the masticatory apparatus affect food processing can help elucidate the selective pressures influencing the evolution of tooth shape.

This general approach assumes that the morphology of the skull and/or teeth can constrain diet, for example, that there are detectable, available, palatable, and nutritious food items that an animal is unable to acquire or process because of limitations to its structural design. Few studies have rigorously tested this assumption for any vertebrates (but see Kiltie 1982, Moore and Sanson 1995; Wainwright 1987). *Pteronotus parnellii*, for example, can readily capture tethered beetles whose exoskeletons it is unable to puncture (Goldman and Henson 1977). Independent measures of the hardness of prey and limitations imposed by tooth morphology would be extremely useful to determine the range of prey types functionally available to various bats.

To date, there have been few studies of any kind that empirically quantify the mechanical properties of bat prey. In an important first step, Freeman 1 (1981a) qualitatively partitioned various insect orders commonly eaten by bats into five hardness categories, ranging from the softest (e.g., Ephemeroptera) to hardest (Coleoptera). Further refinements of this approach might also account for the possibility that hardness varies within orders, at least in part in relation to body size, among different anatomical regions (e.g., odonate heads would be harder than abdominal segments) and among developmental stages. Understanding the mechanical nature of insect cuticle, a tissue commonly con-

sumed by bats, is complicated, however, by the complex nature of its physical properties. Cuticle is a fibrous composite material like plywood and varies in its stiffness and toughness depending on its moisture content (Vincent 1980). The mechanics of hard tissues in noninsect arthropods may be even more complex, as they often incorporate mineral salts into the cuticular tissue, thereby increasing hardness and strength (Vincent 1980).

Only a few studies have addressed the issue of how teeth process different types of foods, although biomechanical approaches hold much promise in this arena. For example, reducing the contact area between teeth and prey increases the local stresses at the contact interface and, thereby, decreases the force required to fracture exoskeletons of prey (Evans and Sanson 1998; Freeman and Weins 1997; Popowics and Fortelius 1997). Strait (1993) predicted that species that feed on hard prey should have relatively short shearing surfaces and found that comparisons of the length of shearing crests on second molars from diverse insectivorous mammals, including bats, supported this hypothesis (but see Evans and Sanson 1998). Such mechanically advantageous localization of tooth/cuticle contact may thus have influenced the structural design of the teeth of diverse insectivorous mammals, including bats.

Determining whether variation in tooth morphology leads to differences in food processing mechanics can effectively test theoretical analyses. In studies of the relationship between the shape of bat teeth and their ability to puncture an apple, teeth with sharper tips required lower puncture force than those with blunt tips (Freeman and Weins 1997). These results have been further refined with large two-dimensional, Plexiglas scale models of teeth with either sharp or blunt tips and a beam-shaped model substrate. For a given load, stresses were more highly concentrated at the point of contact for a smaller than for a larger apical radius—that is, stresses are more concentrated by sharp tips (Freeman and Wiens 1997). This study represents some of the first experimental work to quantify puncture performance relative to apical sharpness of teeth.

Evans and Sanson (1998) also used physical models to test directly the efficiency of different tooth shapes in breaking down foods of varying physical properties. With models that varied in tip sharpness (radius of apical curvature) and cusp sharpness (volume or surface area of tooth per unit distance from apex of cusp), force, and energy required to puncture the cuticular surfaces of beetles decreased with decreasing contact area. These results also highlight the importance of size considerations in comparative studies of tooth morphology; similarly shaped teeth of different sizes will not puncture foods with equal efficiency.

Studies of mastication (e.g., Storch 1968) and analytical predictions of bite forces (e.g., Reduker 1983) have also provided important bases from which to form hypotheses about functional consequences of morphology. For example,

estimates of mechanical advantage for major muscle complexes involved in jaw adduction based on skull and dentary measurements, coupled with estimates of adductive muscle force, suggest that *Myotis evotis*, a substrate gleaner, has a more forceful and quicker bite than *M. volans*, an aerial insectivore (table 6.1). Direct measurement of bite forces of live *M. evotis* and *M. volans*, coupled with analyses of jaw motion during insect capture, would be particularly useful in elucidating this case.

Feeding analyses using electromyography, cineradiography, or measurement of associated forces applied by the jaw muscles during mastication have been limited to only a few studies in bats (e.g., De Guelldre and De Vree 1984, 1990; Kallen and Gans 1972). De Guelldre and De Vree (1990) created a three-dimensional model to estimate applied and reaction forces at the bite point and temporomandibular joints in response to foods of different consistencies in *Pteropus giganteus*. Their kinematic and biomechanical analysis showed that food consistency affected both the magnitude and orientation of the bite force. In particular, the differences between the magnitude of masseter and temporalis activities influenced both the orientation of the bite force and the mechanically optimal position of food. Their conclusions could not have been reached without experimental determination of the sequence in which the muscles fire and their anatomical placement with respect to the jaw joint (De Guelldre and De Vree 1988).

Experimental Approaches to Understanding Ecomorphology of Flight

Experimental approaches are critical to a better understanding of the relationship between flight performance and morphology. Conventional aerodynamic theory has provided a starting point from which to generate hypotheses about the functional significance of the diversity of wing morphologies among species. However, bat wings are structurally complex compared to wings of conventional aircraft. In comparison with aircraft materials, the constituent tissues of wings, skin, muscles, ligaments, tendons and bones are highly variable, nonlinear, and anisotropic in mechanical properties (Papadimitriou et al. 1996; Swartz 1998; Swartz et al. 1996). Moreover, to date, studies of wing morphology are based on fully outstretched wings that represent the minimum wing loading achieved during the wingbeat. Three-dimensional wing conformation, wing mass distribution, and mechanical characteristics of wing tissues also change dynamically throughout even a single wingbeat cycle (fig. 6.5) of an animal flying horizontally at constant velocity (Swartz 1998). The functional significance of wing morphologies of bats and other flying animals will likely best be defined in the context of flapping kinematics. To the extent that one can test the limits of performance abilities associated with particular morphologies, it will be possible to gain deeper insight into

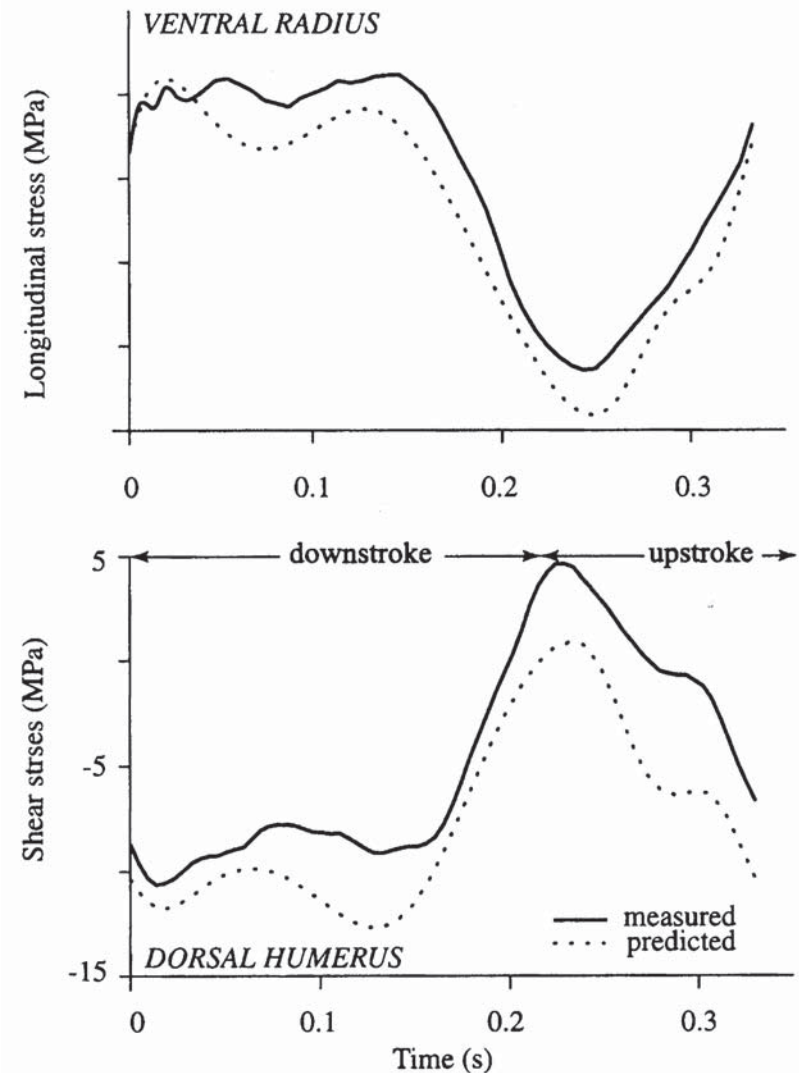


Figure 6.5. A, Dorsal humerus; B, ventral radius. The stress developed on the surface of major wing bones of *Pteropus poliocephalus* during a complete wingbeat cycle (downstroke from $t = 0$ s to $t = 0.22$ s, upstroke from $t = 0.23$ s to $t = 0.34$ s). Empirical values (heavy black lines) are computed from data measured directly from bone surfaces using in vivo implantation of strain gauges onto wild-caught animals; model values are estimated from an abstract computer model of bat flight (see Watts et al. 2001).

mechanical or aerodynamic factors that may constrain habitat use or exploitation of food resources. For example, because some habitats, such as the forest understory, can be spatially complex, differences among bat species in maneuverability differences could directly affect habitat use (Aldridge and Rautenbach 1987).

Flight Maneuvers and Maneuverability

Flight performance through an obstacle course is one useful experimental metric of maneuverability (e.g., Aldridge 1986a, Aldridge and Rautenbach 1987; Stockwell 2001). Among several species of insectivorous British bats, those species best able to negotiate the most tightly spaced string-array obstacles also foraged in the most cluttered habitats (Aldridge 1986b). Similarly, in several species of African microchiropterans, wing loading and body mass were negatively correlated with obstacle course maneuverability, and foraging in habitats of great vegetation density was positively related to maneuverability (Aldridge and Rautenbach 1987). In Neotropical phyllostomids, morphological variables associated with body size (e.g., mass, length of forearm, and wing span) were negatively correlated with maneuverability in an obstacle course in which obstacle spacing was scaled to wing span—that is, larger species were less maneuverable than smaller species, even when performance tasks accounted for absolute variation in wing span (Stockwell 2001). Morphological variables associated with depth of maximum wing camber were positively correlated with maneuverability. The most maneuverable species in the obstacle course were relatively small understory frugivores (*Carollia perspicillata* and *C. castanea*) with wings that could be cambered deeply. In contrast, less maneuverable large canopy frugivores, *Artibeus jamaicensis* and *A. lituratus*, had wings of shallow maximum camber (Stockwell 2001; table 6.1).

Insight into the morphological and behavioral determinants of maneuverability is central to understanding the variation among species in performing maneuvers. At least two strategies for maneuverable flight have been proposed (Thollesson and Norberg 1991). Mass moments of inertia—measures of the distribution of mass in the body and wings with respect to a particular axis of rotation, such as the body's midline—are a major influence on turning ability, at least for rolling turns while wings are maximally extended. For maneuverability at high flight speeds, small roll moments of inertia—wing mass concentrated proximally with minimal mass in the hand wing—are favored to achieve high roll accelerations. Turn radius can also be decreased if body mass and hence wing loading are small. Bats flying at slow speeds, however, can achieve high roll accelerations in spite of high roll moments of inertia when wing mass is concentrated more distally, with relatively heavier dactylopatagia and relatively lighter plagiopatagia. Several slow-flying taxa possess broad wings and wide wing tips that generate extra lift necessary to produce the

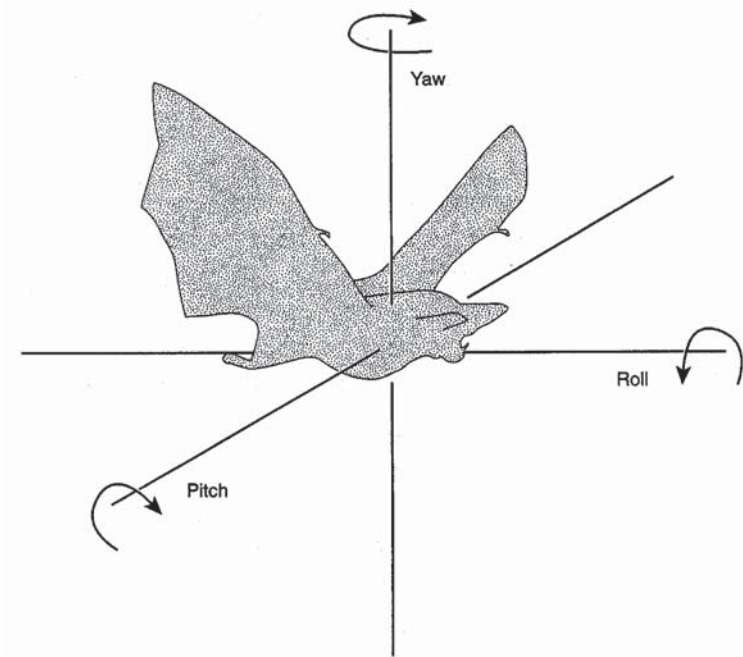


Figure 6.6. Schematic of a bat in flight demonstrating the three rotational degrees of freedom that must be controlled during flight. Roll refers to rotations about an axis passing through the animal's center of mass from head to tail in a horizontal plane, pitch to rotations about an axis that passes mediolaterally in a horizontal plane, and yaw to rotations about a vertical axis. (Adapted from Stockwell 2001.)

aerodynamic moment about the roll axis (Thollesson and Norberg 1991). Thus, a number of aspects of wing shape, including mass distribution along the wingspan and the chordwise dimensions of the wing, interact to influence turning performance. As we gain increasingly detailed information on wing kinematics in both straight and maneuvering flight, the relative importance of these and other yet unidentified design criteria will become clearer.

Many maneuvers by bats are not simple rolls but, rather, also involve pitching and yawing moments (Norberg 1976a; Stockwell 2001; fig. 6.6). Moreover, flapping affects aerodynamic stability because wing movements constantly change the spatial location of the center of aerodynamic force relative to center of mass (Stockwell 2001). Realistic and biologically meaningful comparisons of maneuverability among species must ultimately examine variation in

stability about roll, pitch, and yaw axes to describe the functionally significant aspects of bat flight adequately.

It is increasingly evident that both wing morphology and flight kinematics are important determinants of maneuverability, although, to date, we have little real knowledge of their relative importance. It is clear, for example, that modulation of wingbeat kinematics may allow for the exploitation of a novel or seasonal resource that would not otherwise be predicted based on fixed wing morphology alone. Whether a bat flaps its wings or glides though a turn affects turning performance, and one simple kinematic variable that affects turning performance is the relative proportions of the turn through which wings flap or are held relatively stationary. Among six species of British bats, only *Rhinolophus ferrumequinum* flapped its wings while turning and, as a result, achieved tighter turns than predicted based on morphology alone (Aldridge 1987). Thus, it appears that adjustments of flight kinematics can enable a typically less maneuverable species to negotiate a cluttered habitat or turn tightly in at least some circumstances. The energetic costs and mechanical demands of such short-term adjustments to kinematics are unexplored to date and must be weighed against any gains in maneuverability. We advocate expanding views of what determines flight maneuverability and propose that a more complete understanding of wing movements in relation to flight will also require consideration of important biological functions distinct from flight per se. For example, emission of echolocation pulses, especially in aerial insectivores is coupled with wingbeat (Jones 1994; Kalko and Schnitzler 1989; Lancaster et al. 1995). The coordination of these two major functions must produce as yet poorly understood and complex interactions among aerodynamics, wing kinematics, echolocation, and energetic costs of flight behaviors.

Experimental Manipulation of Body Mass

A number of investigators have explored the limits of flight performance by experimentally manipulating body mass and hence wing loading. Body mass changes substantially on a daily or seasonal basis due to fluctuations in stomach contents, transport of food and young, and so forth. The influence of body mass on flight mechanics and energetics is thus particularly pertinent (Hughes and Rayner 1991; Hughes et al. 1995; Norberg and Fenton 1988; Norberg and Rayner 1987; Schutt et al. 1997; Webb et al. 1992). In a pioneering study of flight performance in five species of North American bats, Davis and Cockrum (1964) found that *Tadarida brasiliensis* took off with loads of no more than 9% of its body mass, in contrast to *Plecotus townsendi*, which readily took off with loads up to 70% of unloaded body mass (table 6.1). More recent work demonstrates that loads as small as 5% of unloaded body mass can result in a substantial loss of maneuverability (Aldridge and Brigham 1988). The decreased maneuverability with increasing wing loading in individuals mirrors the overall pattern seen in broad interspecific comparisons over a large range of body sizes (Aldridge and Rautenbach 1987).

Artificial loading also affects flight kinematics (Hughes and Rayner 1991). Wingbeat frequency and amplitude are greater in artificially loaded than in unloaded *Plecotus auritus* during steady, forward flight, in keeping with theoretical predictions (Hughes and Rayner 1991). In contrast to predictions, flight speed decreases, approximately doubling the predicted power requirements for flight. Such results illustrate the potential impact of changes in total body mass on flight energetics as mediated by subtle changes in wing loading and kinematics.

Computer Modeling Approaches in Ecomorphology

Computer modeling approaches made more accessible by increasing computer power and ease of use can effectively address the functional significance of morphology and kinematics in bats. In particular, when a biologically important behavior can be characterized as resulting from the mechanical workings of a morphological system, computer programs can reproduce organismal function in simplified fashion, sometimes with a high degree of accuracy and precision. This approach offers several important strengths. One can rarely isolate or manipulate single morphological features for functional analysis; it is impossible to alter experimentally the stiffness or strength of structural tissues such as teeth or bone or to induce an individual to activate only a single muscle. However, computer models built on detailed information from living organisms, which thereby reflect biological reality, are not limited in this way. Individual elements of models can be manipulated in ways that the investigator hypothesizes will significantly influence performance. Kinematic patterns that have not been observed in real animals can be imposed on model systems, force magnitudes and orientations can be altered, the size and shape of support elements can be controlled. Computer modeling approaches also enable one to construct potential evolutionary intermediates or extreme forms not represented in extant faunas. For example, one could postulate that the maximum body size of bats is limited by the ability of the bones of the wing to withstand bending stresses imposed by flapping flight or that the diet of a species is limited because it is mechanically unable to process certain food items. Computer models make it possible to assess whether such hypotheses are reasonable and can identify morphological characteristics that dictate performance.

Computer Modeling of the Mechanics and Aerodynamics of Bat Flight

Many components of wing structure have the potential to affect the range of velocities that a species can employ, the energetic cost of flight behaviors, and the aerodynamic forces experienced by a bat. Particularly important design elements include the distribution of mass and lifting surface area along the length of the wing, placement of the bones and muscles within the wing

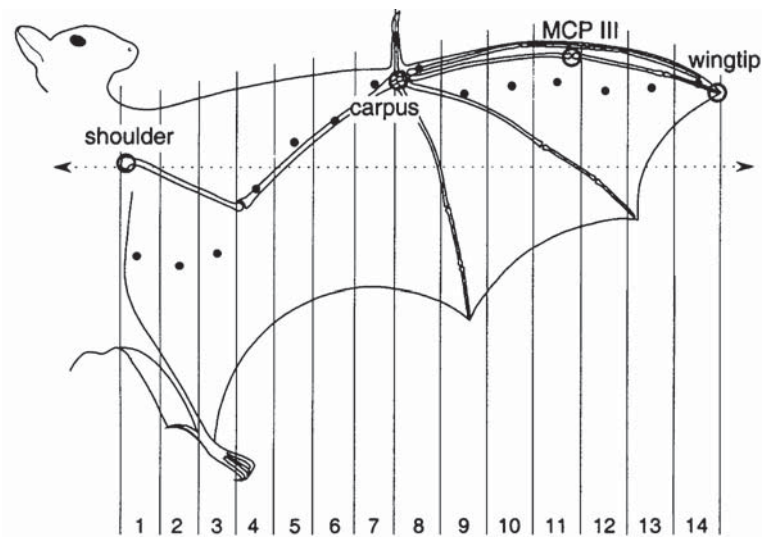


Figure 6.7. Plan-view of the ventral surface of the wing of a *Pteropus poliocephalus* held in a position similar to that of mid-downstroke, showing the subdivision of the wing into 14 chordwise strips for the purpose of computer modeling. The filled circles indicate the locations of the centers of masses of these strips relative to a reference line connecting the two shoulders. The open circles indicate anatomical locations used as landmarks for collecting kinematic data.

membrane, the relative lengths and orientations of various skeletal elements, and the structure of the wing membrane skin. The three-dimensional movements of wing elements interact with this complex structural organization to determine flight performance. To date, our understanding of the specific roles of various aspects of morphology or of kinematics on flight mechanics and energetics remains quite limited, in part because of the near impossibility of experimentally manipulating single parameters of interest, separating them from their normal network of biological interactions.

Computer modeling of the details of the mechanics and aerodynamics of the wingbeat can probe relationships among morphology, kinematics, and wing structural mechanics (Watts et al. 2001). One recent model is based on the morphology and wing kinematics of *Pteropus poliocephalus*, a species whose flight is well studied (Carpenter 1985; Swartz et al. 1992; Thomas 1975, 1981). The model comprises an abstraction of a bat composed of numerous interconnected wing and body segments that reflect anatomy with high precision (fig. 6.7). In particular, model segments accurately reflect the distribution of wing mass and surface area. The model mathematically imposes move-

ments of the wing landmarks through the three-dimensional space based on empirically measured patterns of wing motion based on films of wind tunnel flights.

Building on morphology—a characterization of wing form designed from features likely critical for flight performance—and kinematics, this model computes the magnitude and orientation of each of the forces (gravity, inertia, lift, drag, internal force carried by wing structures, added mass force) acting on each wing segment at small increments of the wingbeat. From the resulting force estimates, it is possible to test the model's validity in two independent ways. First, the model calculates the rise and fall of the bat's center of mass during the downstroke and upstroke respectively. Second, it computes stresses developed in the proximal wing bones. These results can then be compared directly to (1) whole body movements measured directly from films and (2) stress magnitude and orientations measured *in vivo* from strain gauge recordings from the same wing bones in the same species (Swartz et al. 1992; Watts et al. 2001; figs. 6.5, 6.8, and 6.9). For horizontal flight at moderate speed, the model and empirical data match extremely well, providing good evidence that the model captures many of the most important aspects of flight mechanics and aerodynamics in this species. Once the accuracy and precision of the model are validated in this way, the model can be employed to compute measures of energetics, maneuverability, joint forces, and so on with confidence. Future analyses that employ realistic models such as this one, which can be extended to diverse species, will allow exploration of many questions of interest to the ecomorphology of bats: functional significance of wing mass and area distributions, aerodynamic and/or mechanical limits on body size, energetic consequences of load carrying, and many others.

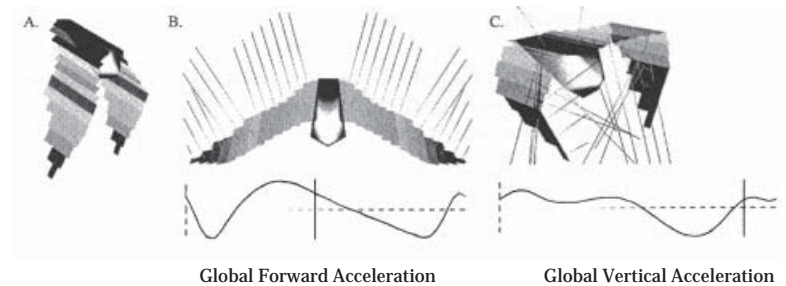


Figure 6.8. Single frame images from dynamic visualization of computer model of bat flight. *A*, Animation allows the user to view the bat from any position and at any degree of zoom (mouse controlled) as the wings beat. *B*, Distribution of lift on the wing: users may select a single wing force and display its vector representation on each segment from any view; these vectors change dynamically in concert with a display of the forward or vertical acceleration of the center of mass (bottom: vertical bar moves horizontally with wingbeat cycle). *C*, Total force on the wing: any combination of forces may be selected (here portions of the vectors are off the figure).

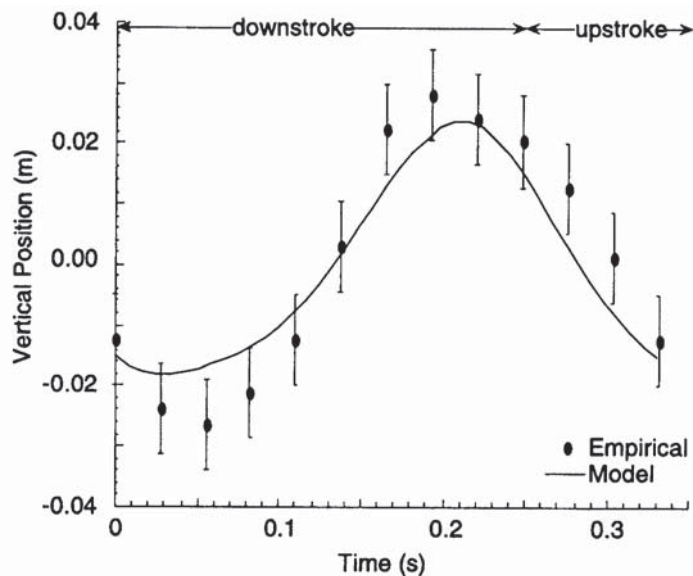


Figure 6.9. Comparison of the vertical oscillations of the bat's center of mass over one wingbeat cycle as computed from the model (solid line) and as measured directly from wind-tunnel film footage (filled circles; bars represent 2 SDs).

Computer Models and Analysis of Tooth Morphology

Teeth must successfully process different foods, and, for bats, teeth take the form of slicing blades, crushing devices, juice extractors, et cetera (Lucas 1979). The relationship between tooth form and diet in bats is well exemplified by an example of a dietary type not observed among any other mammals: blood feeding in the vampire bats. Desmodontines, obligate sanguivores, have no need to mechanically process their food and possess small, razor-sharp, blade-like incisors that can readily inflict superficial wounds, and yet their teeth appear unable to withstand the stresses normally generated during biting or chewing (Freeman 1992; Van Valkenburgh and Ruff 1987).

For most bats, however, the interplay between tooth form and diet is complex. Effectiveness of a particular tooth morphology in puncturing hard-bodied prey items will depend on the size and shape of the puncturing teeth, the size and hardness of prey items, and the magnitude of muscle force that can be recruited for biting as amplified by the lever mechanics of the jaws. These design considerations must then be balanced against competing design constraints. For a given amount of bite force applied to a jaw, long, very sharp blades or cusps can generate very high, localized stresses in whatever an animal bites but have a greatly increased risk of breakage.

How can one realistically assess the role of shape in tooth performance? The morphology of mammalian teeth is more complex than the human-manufactured structures to which classic engineering design theory can be readily applied. A relatively new engineering analysis technique, finite element analysis, is, however, well suited to this problem (Beaupre and Carter 1992; Huiskes and Chao 1983; Zienkiewicz and Taylor 1989). In finite element analysis (FEA), complex geometries are redefined as composites of a large number of simple shapes, each of which can be analyzed using conventional beam theory. The mechanical response of each of these simple shapes to applied forces can be readily calculated, and mathematical algorithms employed to link results among the many component elements, thereby estimating mechanical behavior of the whole structure (Zienkiewicz and Taylor 1989). How accurately a combination of many simple forms reproduces a complicated and irregular geometry depends largely on the number of elements employed; partitioning of a complex shape into 100 relatively large elements will not provide the same precision of analysis as dividing the same shape into 10,000 elements that are each 100-fold smaller. However, it takes far more computational time and power to analyze models with many thousands of elements than those with a few. This approach provides a powerful way to gain insight into the mechanics of structures of complex shape and holds great promise for the study of biological structure.

Freeman (1998) used FEA to examine the effects of tooth shape on the propagation of cracks through a food substance as the tooth penetrated the food and compared the effects of an edged versus a nonedged canine tooth as it penetrated a uniform substance. Stresses were highest at the margins of the edged tooth model and, in contrast, were less but were uniformly distributed around the nonedged tooth model. To validate results from the finite element model, Freeman (1998) constructed scale models representing edged and non-edged teeth and applied them to a pressure-sensitive, photoelastic material to simulate biting into food. Preliminary results of this physical modeling are consistent with and lend strength to the PEA simulation results. Both approaches document a substantial increase of surface energy at the edge of a puncture initiated by an edged tooth, and no such build-up with a nonedged or circular tooth. Further experiments will examine more subtle shapes of teeth and will extend this analysis to three dimensions.

Phylogenetic Considerations in Ecomorphology

Several recent studies emphasize the importance of interpreting interspecific variation in morphology in the context of well-defined phylogenies (reviewed in Losos and Miles 1994). Unless clear cases of convergence in morphology are demonstrated among distantly related taxa, the mechanism underlying a

particular morphological trait will remain obscure. Variation in degree of phylogenetic relationship among taxa will, in and of itself, produce patterned morphological variation, and explicit efforts are needed to distinguish morphological similarity due to similar selective pressures from that due to shared ancestry alone. Multiple independent evolutions of particular characteristics, or convergences, can be especially illuminating in this context.

A clear case of convergence in both tooth and flight morphologies associated with the evolution of carnivory (feeding on vertebrates as opposed to invertebrates) has been demonstrated among species of Nycteridae, Megadermatidae, Vespertilionidae, and Phyllostomidae (Freeman 1984; Norberg and Fenton 1988; fig. 6.2). Because these families are relatively distantly related (Baker et al. 1989; Koopman 1984; Pierson 1986; Simmons 1998; Smith 1976), low wing loadings and low aspect ratios of carnivorous members of these four families appear to have evolved independently under similar selection pressures for slow, maneuverable flight and the ability to carry heavy prey. The independent acquisition of particular morphological features in the distinct lineages provides more compelling evidence for a functional relationship between these morphological traits and the flight behavior associated carnivorous bats than would be possible in the absence of phylogenetic context.

Phylogenetic mapping of morphological traits in bats is exemplified by recent work superimposing a phylogeny of the family Phyllostomidae onto ecologically important craniodental characteristics (Baker et al. 1989; Freeman 2000; fig. 6.4). This coupling of morphology and phylogeny leads to a better understanding of the adaptive radiation of the phyllostomids, in particular, and the evolution of Microchiroptera, in general. Microchiropteran bats are overwhelmingly insectivorous and constraints on morphology imposed by insectivory have produced a dynamic equilibrium in bat morphologies that has persisted for 60 million years. The morphological diversification within phyllostomids is greater than in all other families of microchiropteran bats, and although many phyllostomid lineages have undergone substantial change, those that have maintained insectivory have changed little (Freeman 2000). This mapping approach suggests that the ability to eat fruit may be the key synapomorphy that has facilitated phyllostomid ecological and morphological diversity. In addition, this study demonstrated that morphology, ecology, and phylogenetics can be effectively integrated to deepen our understanding of bat evolution.

Conclusions

Studies that have identified patterns of association between morphology and behavior (e.g., Freeman 1981a; Norberg and Rayner 1987) have provided a big-picture view of the ecomorphology of flight and feeding and serve as impor-

tant foundations from which to generate new hypotheses about the function of morphological traits and factors that might have influenced bat evolution. There are many gaps in current knowledge about bat ecomorphological relationships, and many of the patterns of morphological differences and associated behaviors have yet to be experimentally tested or quantified. It is our hope that the approaches we have outlined in this chapter will aid in the design of future studies. Future field studies will continue to expand our knowledge of the ecology and behavior of bats in their natural environments, and experimental work and detailed kinematic studies can help test theories based on mechanics or fixed-wing aerodynamics. In cases where experiments are difficult to conduct on live animals, computer modeling provides a new tool with which to understand better the mechanical limitations imposed by morphology and to help identify functionally important morphological characters.

How, then, can we best study the ecomorphology of bats? Integration of field and laboratory methods and collaborations among ecologists and morphologists are integral to future progress. Time-consuming and labor-intensive research will be of greatest value when it addresses questions that are relevant to better understanding of both the morphology of bats and the ecological significance of morphology. Morphological and experimental studies that focus on traits of known ecological importance are particularly valuable, as are ecological studies that highlight behaviors whose mechanistic basis is well understood. The effects of body size on interspecific patterns, intraspecific variation in ecology and morphology, and phylogenetic effects on observed patterns of structural and behavioral variation have yet to be fully addressed. In all, we believe this field will advance rapidly in coming years, as new insights into the ecomorphology of bats arise from increasingly successful synthesis of morphological and ecological study.

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